The biomechanics of sensory organs

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Synopsis Studies of mechanosensory systems have largely focused on the filter characteristics of their neural components in relation to their ultimate function. Less attention has focused on the role of the physical structure of the sensory organ which also acts as a mechanical filter of the sensory input. This biomechanical filtering is readily apparent in the case of several mechanosensory systems that transduce information about the deformations of the sensory organs in response to external forces. Because these deformations critically depend on the geometry and material properties of the mechanosensory organs, it is necessary to conduct focused studies on the biomechanical characteristics of these organs when studying the encoding properties of the mechanosensory system. Modern experimental tools such as Laser Doppler Vibrometry and computational tools such as Computational Fluid Dynamics and Finite Element Analysis provide the means for determining the sensory pre-filtering properties of small-scale mechanosensory structures. In all the cases covered in this review, the physical properties of the sensory organs play a central role in determining the signals received by the nervous system.

Introduction

The information that an animal acquires about its surroundings is filtered through its sensory apparatus. This filtering is influenced by the material and geometric architecture of a sensory organ and its underlying nervous system. Although the neural circuitry is the focus of most studies of how the sensory system detects environmental information, there is relatively little emphasis on the role of the structural properties of sensory organs or the medium surrounding the organ in modifying sensory inputs. Yet, biomechanical filtering often has profound implications for the animal's ability to sense a stimulus and in several cases the material architecture of sensory organs is finely tuned to signals of ecological relevance. Thus, their structural biomechanics constitute an essential component of their ultimate function (Fig. 1).

Despite their potential importance, little is known about the mechanical properties of most sensory organs. This gap in knowledge likely stems from the traditional division between the fields of comparative biomechanics and sensory neurobiology. Here, we provide an overview of studies that have specifically focused on the biomechanics of mechanosensory systems. This body of research combines biomechanical and neurobiological principles to address the challenges faced by animals as they sense structural strain, the flow of air or water, and sound. We highlight recent developments in these diverse systems to underscore the importance of an integrated approach when addressing how animals acquire information about their physical environment. Although this review primarily focuses on mechanosensory systems, such an integrated approach is also important in understanding the function of other sensory modalities. Rather than focus on various sensory systems in a taxon-specific manner, we have chosen to highlight the sensory challenges and our knowledge of how these are resolved in diverse taxa. In the process, we describe the main technical challenges facing research on the biomechanics of sensory organs to help identify areas of fruitful collaboration between researchers working in the areas of biomechanics, mechanical engineering, and neurobiology.

Sensory challenges

Sensing cuticular strains

The stiff exoskeleton of an arthropod challenges the animal's ability to detect external physical forces on its body. Arthropods have evolved multiple
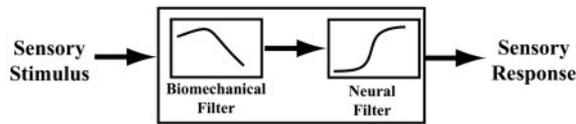
Fig. 1 A flow diagram depicting the paradigm of sensory biomechanics. The traditional neural filter is subdivided into a biomechanical and a neural filter, to reflect the mutually exclusive roles of these two components.

mechanosensory structures that detect the exoskeletal strains caused by external forces. These include campaniform sensilla (Fig. 2A and B) and lyriform organs (Fig. 3A–C), that are located on the surface of the exoskeleton and which are lined internally with the dendritic arbors of sensory neurons. As described below, the strain-sensing ability of these structures derives from the concentration and amplification of the strains on the cuticle arising from regions of material discontinuity in the exoskeleton. In addition to exoskeletal structures, insects and crustaceans also detect movements between joints using internal mechanosensors called chordotonal organs (for a detailed review, see Field and Matheson, 1998), the discussion of which is beyond the scope of the current review.

Campaniform sensilla

Arthropods sense cuticular stresses using mechanosensory receptors called *Campaniform sensilla*, which are composed of cuticle and of sensory cells (Fig. 2A and B). In insects, these organs occur either as a single sensillum [e.g. on the wings of flies (Dickinson, 1992)], irregularly arranged fields (e.g. on the legs of a cockroach) (Pringle, 1938b), or a regular pattern of sensilla (e.g. on the base of fly halteres; Fig. 2A; Pringle, 1948). Each organ contains a small (on the order of 10 μm) campaniform cap situated at the center of a circular or oval indentation in the cuticle. In most cases, the cap is composed of a stiff exoskeletal layer that overlays a spongy cuticular layer. The spongy layer and the cap membrane are both highly extensible and thought to contain the elastic rubber protein resilin, based on their mechanical and biochemical properties (Thurm, 1964). The different components of each campaniform sensillum have vastly different material properties. The elastic modulus of the cuticular cap (6 GPa) is 600 times that of the cuticular membrane (10 MPa), which is five times more stiff than the spongy cuticle. This structure is connected to the dendritic ends of a bipolar sensory neuron *via* an intermediate structure called the tubular body, which consists of a bundle of microtubules

(Thurm, 1964). Sensitivity of the campaniform sensillum is thus a function both of local geometry and of composite material properties of the cuticle.

Since Pringle's first demonstration that campaniform sensilla are primary sensors of cuticular strain (Pringle, 1938a, b), it is increasingly evident that amplification of the tiny strains is first facilitated by the biomechanics of campaniform structure. The forces acting on the cuticle surrounding the campaniform sensillum are transformed by the geometry of the campaniform sensilla into an up-and-down motion of the bell-shaped cap. This motion is transduced by the underlying sensory neuron into graded or action potentials with nanometer-scale sensitivity (Fig. 2B) (Chapman, 1965; Dickinson, 1990). The overall geometry of the campaniform sensillum influences the directional sensitivity of this transduction. For example, an oval-shaped organ is most sensitive to stresses acting at right angles to their major axis, whereas circular campaniform sensilla respond to strains equally from all directions. In many insect structures, such as the wing hinge or the haltere base, which have complex geometries (Fig. 2A), the measurement and modeling of the *in vivo* strain patterns in these regions poses a major technical challenge.

Barring a few efforts to directly measure the strains with strain gauges (Blickhan and Barth, 1985), there have been very few attempts to determine cuticular strains as a means of understanding the degree of biomechanical filtering in the campaniform sensilla. In absence of such data, it is not possible to determine the precise nature of the stimuli experienced by the individual or even by a field of sensory neurons. As a result, researchers have largely relied on numerical (Skordos et al., 2002; Vincent et al., 2007) or analytical (Cocatre-Zilgien and Delcomyn, 1999) modeling to understand how applied forces transform into strain fields around the campaniform sensilla. Such models have usually assumed a simplified shape because measurements of the geometry of the campaniform sensilla and their surrounding region are sparse.

On the numerical front, Skordos et al. (2002) have developed a Finite Element Model of a specific campaniform sensillum in the blowfly, *Calliphora vicina*. This model of a particular campaniform (the pG4 sensillum from the posterior of the mesothoracic leg; also see Gnatzy et al., 1987; Grunert and Gnatzy, 1987) enables investigation of the mechanical contributions of the campaniform cap, its surrounding collar, the joint membrane and an annular compliant socket septum with its spongy compliant tissue. In this study, the cuticle-campaniform
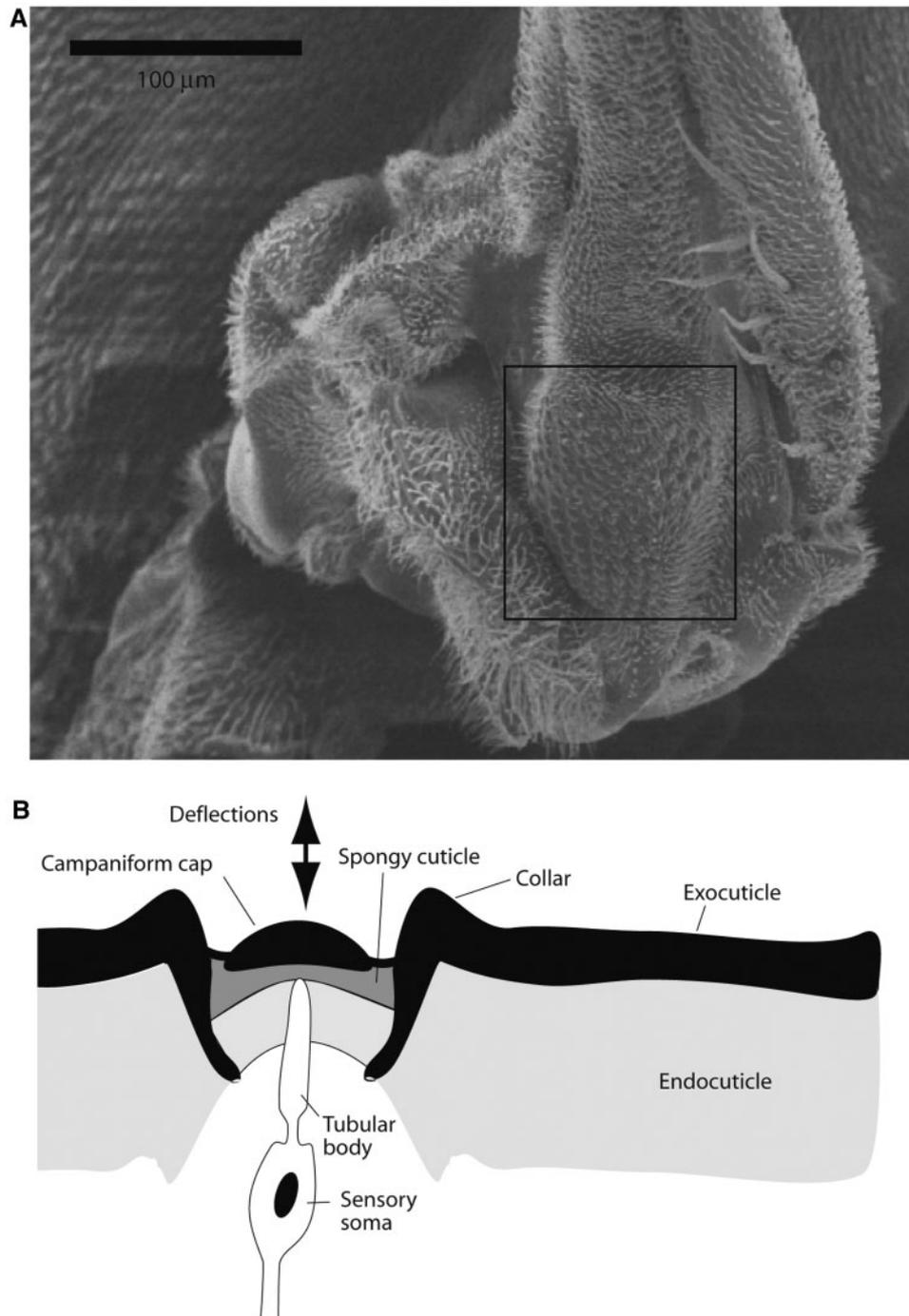
Fig. 2 (**A**) The base of the haltere of the dipteran, *Hermetia illucens*. Inset shows the regularly arranged fields of campaniform sensilla. Scale bar corresponds to 100 μm. (**B**) A diagram of the cross-section of a campaniform sensillum.

system was initially modeled as a 2D flat plate with an oval hole to address how the presence of such holes influences the strain patterns on the cuticle. Skordos et al.'s study showed that the global stiffness of the cuticle is unlikely to be greatly affected by the presence of campaniform sensilla. However, the local deformations are greatly amplified in the region around the campaniform "holes" in response to broadly applied forces. This stress-intensification explains why any perforated tissue is more likely to tear at the perforations rather than in the non-perforated area. Thus, it appears that detection of cuticular stresses relies on the amplification of these stresses by concentrating them through mechanical discontinuities created by a single, or a group of, campaniform sensilla. Furthermore, the

thickening of cuticle along the collar of the campaniform sensilla may help prevent the tissue from tearing at these sites.

Skordos et al. (2002) further extended their model to 3D so as to include various components of the campaniform and its surrounding geometry. Although the data on material properties of various components of a campaniform sensillum were not available, the authors were able to use the staining characteristics of the tissue to infer the material properties and composition of various parts of the tissue. Their 3D campaniform model suggested that the architecture of a campaniform sensillum amplifies the applied stress signal above that which can be achieved merely by the material discontinuity in the cuticle around the organ. In this model, alterations in material properties of the joint membrane, the cuticular cap, or the spongy cuticle had very little influence on this coupling mechanism. However, the material stiffness of the surrounding collar made a significant difference to the output of the campaniform. This suggests that collar mechanics may be the main "tunable" entity from the functional perspective. Therefore, subtle alterations in the thickness or in the degree of tanning of the collar cuticle can enable the campaniform to alter its sensitivity to environmental stresses. Because the outputs of a model of a campaniform sensillum with heterogenous architecture are fundamentally different from that of one with homogenous material, the cuticular microstructure is also of crucial importance. Developing a finite-element model with such composite properties is especially difficult, as the properties of the cuticle vary greatly within the small region surrounding the campaniform. These models are consequently highly dependent on assumptions about the material properties of the sensory structure. Nevertheless, as evident from the above studies, such models are useful in generating several broad functional insights into the function of campaniform sensilla. Recently, Vincent et al. (2007) extended this model to groups of either circular or oval holes to investigate how fields of campaniform sensilla, such as those at the base of a haltere or a wing, may experience the spatial distribution of the applied mechanical stress.

Lyriform organs

Arachnid slit sensilla present another example of strain sensing involving biomechanics of the exoskeleton (Fig. 3A and B). Like the campaniform sensilla, the slit sensory organs are distributed all over the body of arachnids either as single slits or as arrays of slits concentrated in patches near the extremities.

At several locations along the body and limbs, the slit organs occur in parallel groups, loosely resembling the strings of a lyre. This so-called "lyriform organ" has proved particularly amenable to experimentation because of the easy accessibility of the sensory structures, their underlying nervous system, and the efferent arbors that modulate gain of the sensory system (French et al., 2002; Barth, 2004). Each slit is associated with two large bipolar mechanosensory neurons that enable this organ to detect any deformation in the slit created by an external load. This organ is capable of detecting signals like the vibrations induced in a spider's web by insect-prey, mates, or predators. The mechanosensitive channels of the two bipolar neurons lie within the dendritic tips arborizing at the slits. These dendritic tips are surrounded by a Na^+-rich receptor lymph. One neuron extends a process to the outer membrane of the slit and the second one is shorter and connects to the inner membrane (Fig. 3C). Under mechanical stress, the net compression of the lyriform slits on the spider's legs causes the underlying bipolar neurons to generate graded receptor potentials at low strains and action potentials at high strains. (French et al., 2002; Barth, 2004)

The geometry of the lyriform organ is integral to its mechanics and hence to sensitivity to mechanical signals. Its mechanics has been studied extensively, including direct strain measurements (Blickhan and Barth, 1985) and numerical modeling of the regions around lyriform organs (Hößl et al., 2006, 2007). To determine how an external stress distributes through the cuticular lyriform structures, Hößl et al. (2007) developed two models of the slit sensors. The first (Hößl et al., 2006) was an analytical model that treated the slits as interacting fractures through a stiff membrane. This approach assumed that the long, thin slits (length/width ratio ~100) approximate closely spaced and mutually interacting surface cracks. Key to their approach was the approximation of superposition of stress. This means that a plate of cuticle consisting of n cracks and loaded by an external stress may be mathematically treated as a plate containing no cracks linearly superposed with n plates each containing one of the n cracks. Further, each crack experiences stress equivalent to the externally loaded stress and the stresses induced by the presence of other cracks. The results of this model showed some qualitative agreement with data on slit-face displacement as functions of external and internally modified stresses acquired on a mechanical polymer model of arachnid slits (Barth et al., 1984), but this approach suffers from the limitation that the
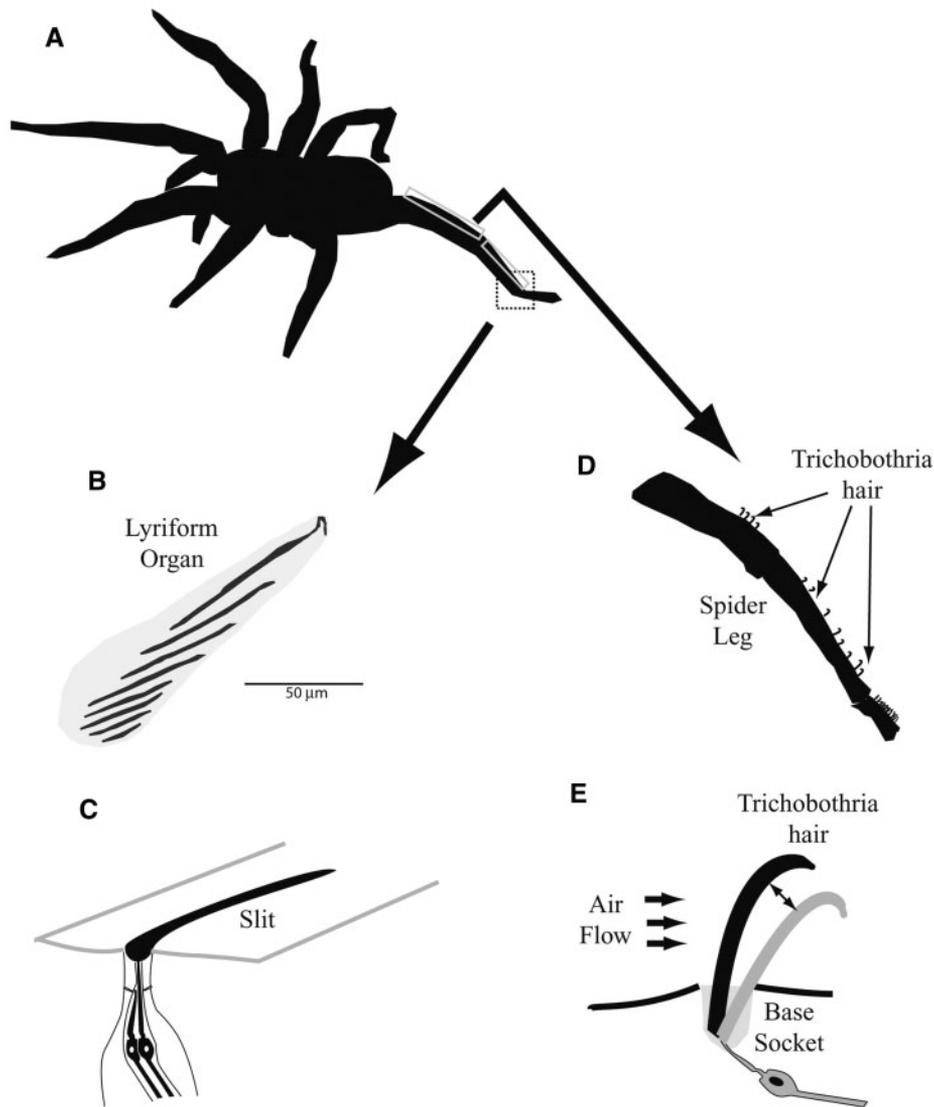
Fig. 3 Arachnid sensory organs. (**A**) Locations of strain and flow sensors on spider legs. These sensors occur on all legs but here are indicated on only one leg. (**B**) The spider lyriform organ (redrawn from a photograph in French et al., 2002). Each black line corresponds to an individual slit in the lyriform organ. The organ depicted here is made from eight slits. (**C**) Cross-sectional view of an individual slit organ. (**D**) Trichobothrial hair along the spider's leg. (**E**) Individual hairs move within their base socket due to external air flow.

slits have to be spaced by at least one-half the length of each slit.

To overcome the limitations of this analytical approach, a finite element model (Hößl et al., 2007) was used to compute the strains around the slit organs based on measured material properties of the cuticle (Barth et al., 1984). In the finite element model, it was possible to place the slits arbitrarily close and determine their influence on each other. Although much simplified, compared to slit sensilla, such models enhance our understanding of the functional consequences of different arrangements of slits. Furthermore, the distribution of strain predicted by such models may be compared to

morphological parameters, e.g. the location of dendritic arbors along the slits. It is thus possible to use these models to understand how exoskeletal strains around the slit organs are transduced by the sensory system.

Sensing the flow of fluids

Animals have independently evolved several mechanosensory strategies that sense the flow of fluids. These include such diverse mechanosensory modalities as the sensory hairs of arachnids (Görner, 1965), cephalic bristles (Weis-Fogh, 1947) and antennae in insects (Heran, 1957), whiskers in mammals (Dehnhardt et al., 1998), and the lateral line system

in fish (Dijkgraaf, 1963; Bleckmann and Rathmeyer, 1994). Because detection of flow informs the animal about approaching predators, self-motion, or unwanted displacement, it may be a key to survival. The dynamics of these organs depend on the size of the animal and the fluid dynamic regime in which they operate. In all these cases, movement in the fluid medium is detected by the deflection of a sensory organ due to an external flow and its subsequent transduction by the underlying sensory neurons. Here we describe sensory organs in insects, arachnids, and fishes to illustrate the role of biomechanics in the sensing of flow.

Filiform hair

In insects from diverse orders such as Orthoptera (crickets) and Blattaria (cockroaches), the task of detecting air flow is carried out by sets of filiform hairs present on the cerci (Fig. 3A and D; also see Fig. 5) (Edwards and Palka, 1974; Palka and Edwards, 1974; Landolfa and Miller, 1995). These hairs have a great range in length (30–1500 μm) and diameter (1.5–9 μm) (Dumpert and Gnatzy, 1977). Because the mechanism of detection of flow depends critically on the mechanical structure of the hair, differences in the lengths of cerci provide the ability to fractionate their response to a wide dynamic range of magnitude of stimulus. This was shown by Shimozawa and Kanou (1984a, b) in a series of experiments that explored the physical and neural basis of range fractionation in the cercal system. By attaching tiny spheres to the hair and using the weight of these spheres to deflect the hair by a known torque, Shimozawa and Kanou (1984a) determined the stiffness of the hair and showed that it increases by a factor of 100 as the hair length varies from ∼100 to ∼1000 μm. When stimulated with air puffs of intensities at the threshold of activity, the hairs showed spiking activity that was dependent on the length of the hair. Shorter hairs had greater activity thresholds with a steeper slope against changes in frequency compared to longer hairs. Hairs longer than 800 μm did not change threshold intensity with frequency; thus, they are velocity-sensitive because their firing depends on the velocity of the air and not on duration of the puff. In contrast, the shorter hairs (<400 μm) changed their firing rates with the time course of the stimulus and were therefore found to be sensitive to acceleration (Shimozawa and Kanou, 1984a).

The neural organization of these sensory hairs directly reflects their function. The sensory arbors of the shorter, acceleration-sensitive hairs project upon a set of phasic (P-type) interneurons. The long velocity-sensitive hairs project upon a set of tonic (or T-type) interneurons. In addition to these interneurons, a set of phaso-tonic interneurons (PT-type) also likely mediate a fast response to a sudden acceleration of the surrounding air. This system is capable of distinguishing between sudden movements due to nearby predators and sustained flows of ambient air. Thus, the range-fractionation properties of the sensory air field in filiform hair owe much to their physical structure (Kanou and Shimozawa, 1984). In addition to the primary sensory system, the encoding properties of the interneurons have also received a very detailed treatment making the cricket cercal system an especially promising system in terms to understanding information encoding from biomechanics to behavior (Miller et al., 1991; Theunissen and Miller, 1991; Theunissen et al., 1996).

Trichobothria

Similar principles apply to the trichobothria on the legs of spiders, which are also highly sensitive to ambient air-flow (Barth, 2004). Like the filiform cercal hair, trichobothria are also present in a range of sizes that affect their spectral sensitivity. The observed range of trichobothria hair roughly match the predictions for the thickness of the boundary layer suggesting that the trichobotria sensory units of different lengths are tuned to detect flows of different velocities (Humphrey et al., 1993). The neurons underlying each trichobothrium have similar tuning properties irrespective of the length of the hair and thus the neural system, by itself, provides only a very coarse filter for the incoming mechanical signals. The fine tuning properties of the trichobothria are dictated primarily by the biomechanics of the hair rather than the underlying nervous system(Barth, 2004).

The biomechanical properties of the trichobothria in the ctenid spider, *Cupiennius salei*, have received rigorous experimental and theoretical (both analytical and numerical) treatment (Barth et al., 1993; Humphrey et al., 1993, 1995; Devarakonda et al., 1996; Barth and Holler, 1999). In these studies, the mechanosensory hairs were broadly modeled as inflexible smooth cylinders. Whereas normal straight bristles were modeled as straight hairs, the spider trichobothria were modeled with the tips of the cylinder bent at 90° to approximate the curved hair of the trichobotria (Fig. 3D and E). By applying the law of conservation of angular momentum to this model hair and accounting for fluid dynamic drag and added mass, this study predicted the spectral sensitivity of the hairs to oscillating external flow.

Specifically, it suggested that at lower frequencies (<200 Hz) longer hairs more effectively encode velocity of flow, whereas at higher frequencies (>200 Hz) shorter hairs are more effective as sensors of velocity and acceleration (Humphrey et al., 1993). These predictions were validated by direct measurements of the air-flow-driven deflection of groups of trichobothria on the tibia, metatarsus, and tarsus (Barth et al., 1993). The comprehensive approach taken by these studies provides a model to guide future studies on sensory biomechanics.

The lateral line system

The lateral line system is an organ in fishes and amphibians that detects the flow of water (Leydig, 1850). Lateral line receptors, called *neuromasts*, include a cluster of mechanosensory hair cells on the surface of the body; these detect flow because of their linkage to a gelatinous structure, the *cupula* (Coombs and Montgomery, 1999). Based on morphological differences, two types of neuromasts have been identified in fishes. In superficial neuromasts, the cupula extends from surface of the body directly into the water, whereas a canal neuromast is recessed within a channel beneath the scales (Fig. 4A and B) (Dijkgraaf, 1963; Montgomery, et al., 1995). The relatively large size of canal neuromasts (~200–600 μm in diameter versus ~30–100 μm for superficial neuromasts; Munz, 1989) and their numerous hair cells have enabled investigators to examine how the interaction of mechanics and neurobiology transforms a flow-stimulus into a nervous pattern (see Windsor and McHenry, 2009; Mogdans et al., 2004; McHenry and van Netten, 2007; Van Trump and McHenry, 2008; Bleckmann, 2008; McHenry et al. 2008 for research on the micromechanics of superficial neuromasts). Here, we consider the role of biomechanics in the filtering of flow signals by canal neuromasts.

Canal neuromasts filter a flow stimulus at many levels. A pressure field around the body generates flow over the body's surface and within the canals (Fig. 4B). Movement of fluid within the canal deflects the cupula (Denton and Gray, 1983, 1989) and this deflection is transduced by the hair cells into graded receptor potentials that are encoded by a train of action potentials along an afferent neuron (Flock, 1965). Each level has the potential to attenuate some components of the frequency of a signal and more effectively transmit others. The role of biomechanics in this filtering may be evaluated by comparing the frequency response predicted by mechanical theory with the action potentials evoked by a vibrating sphere, as measured in trout (*Salmo gairdneri*; Kroese and Schellart, 1992). At each level, frequency responses may be calculated as transfer functions that express sensitivity in terms of the ratio of output to input of the signal (Table 1), assuming that the magnitude of an output is proportional to the input.

Frequency responses for canal neuromasts are most commonly measured with a vibrating sphere as the stimulus source. One benefit to this stimulus is that the pressure field around the sphere is well understood and easily modeled (Stokes, 1851; Harris and van Bergeijk, 1962; Kalmijn, 1988). This model calculates the gradient in pressure along the fish's body for a fixed position of the canal relative to the sphere. Driven by this gradient, there is acceleration of water at the surface (equal to the pressure gradient, divided by water density), thereby generating flow through the canal. Because this signal increases with the square of the stimulus' frequency for a fixed sphere displacement [i.e. $40\,dB\,dec^{-1}$; Fig. 4C(ii)], the acceleration of surface flow is proportional to the sphere's acceleration. The flow signal received at the body's surface is filtered by the hydrodynamics of the canal. Oscillatory flow through a cylindrical pipe is well-described by an analytical model of its hydrodynamics (Sexl 1930; Denton and Gray, 1982, 1983; van Netten, 2006). Using this model (Equation 24 in van Netten, 2006), the sensitivity of velocity of flow within the canal to acceleration of flow at the surface may be calculated. The results of these calculations suggest that for canals of sufficiently small diameter, viscosity dominates the resistance to flow at low frequencies of the stimulus [Fig. 4C(iii)]. As a consequence, the velocity of flow in the canal is directly proportional to the pressure gradient and to the acceleration of the flow at the surface. This relationship is disrupted at higher frequencies, as the fluid's inertia causes velocity to reduce in inverse proportion to frequency (i.e. $-20\,dB\,dec^{-1}$). Thus, the canal serves as a first-order low-pass filter of acceleration at the surface (Denton and Gray, 1983; van Netten, 2006).

An additional biomechanical filter is provided by the fluid and structural dynamics of the cupula. An analytical model of cupular dynamics was developed and tested by nanometer-scale deflection measurements with laser interferometry (van Netten and Kroese, 1987; van Netten, 1988, 1989; van Netten and Khanna, 1994). This model demonstrates that at low frequencies, viscous drag acts to deflect the cupula. The combination of this force and the elastic resistance of the hair cells cause the cupula to deflect in proportion to the velocity of flow in the canal. As the frequency of the stimulus increases, stiffness
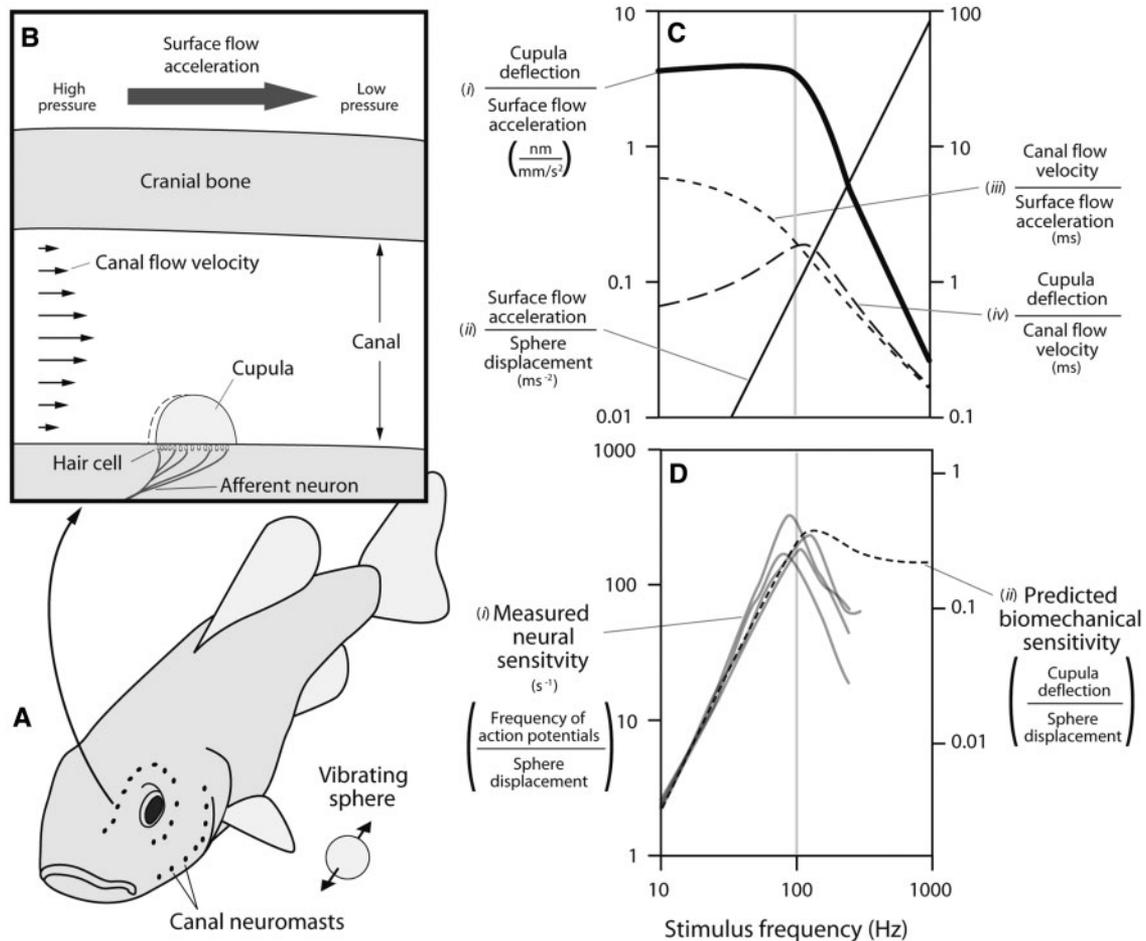
Fig. 4 Biomechanical filtering by canal neuromasts in the lateral line system of fish. (**A**) A fish uses its canal neuromasts to sense the flow generated by a vibrating sphere. (**B**) A detail of one neuromast illustrates an instant of time when the pressure gradient created by the sphere generates flow acceleration at the surface and flow velocity within the canal. The canal flow causes the cupula to deflect, which is encoded by a change in the frequency of action potentials (data not shown) propagating along the afferent neuron. Each of these levels has the potential to filter the signal created by the vibrating sphere. (**C**) Biomechanical filtering is demonstrated by the frequency responses of water flow and cupula deflection: (i) the ratio of cupula deflection to surface flow acceleration (thick line) depends on both the hydrodynamics of the canal and the micromechanics of the cupula; (ii) the ratio of surface flow acceleration to sphere displacement (thin line) is calculated by potential flow theory (van Netten, 2006); (iii) the velocity of flow relative to this acceleration (short dashes) is determined by canal hydrodynamics (Denton and Gray, 1983); and (iv) the ratio of cupula deflection to canal flow velocity (long dashes) is predicted by cupula micromechanics (van Netten and Kroese, 1987, 1989). (**D**) All levels of biomechanical filtering are compared with measurements of the frequency of action potentials excited by a vibrating sphere. (i) Each gray line corresponds to an afferent recording attributed to canal fibers in separate individuals (in *Salmo gairdneri*, Kroese and Schellart, 1992). (ii) The predicted biomechanical sensitivity (dashed line) was calculated as the product of transfer functions for the hydrodynamics of a sphere C(ii), and canal C(iii) and cupula micromechanics C(iv) (for *Gymnocephalus cernuus*, van Netten, 2006).

of the hair cells and the mass of the cupula and the fluid drive the neuromast to resonate (van Netten, 1991). This resonance enables cupular deflections to have an elevated sensitivity at higher frequencies (van Netten, 1991). This model (Equation 13 in van Netten, 2006) may be used to calculate the sensitivity of cupular deflection to the velocity of flow in the canal [Fig. 4C(iv), using parameter values in Table 1]. The rise in sensitivity predicted occurs with a peak at ~115 Hz, which is well within the range of frequencies at which hydrodynamics attenuate the velocity of flow within the canal [Fig. 4C(iii)]. The counter-acting trends of elevated deflection of the cupula and the attenuation of flow velocity within the canal at higher frequencies cause the combined sensitivity of the cupula and canal to remain relatively constant up to ~115 Hz [Fig. 4C(i)]. At greater frequencies, both the cupula and canal contribute equally to a decline in sensitivity (at $-40\,dB\,dec^{-1}$). Thus, the combined influence

Table 1 Mathematical models of mechanical filtering in the canal neuromasts of fish

Transfer function (output/input)	Parameter	Values	Source of model [parameter values]
Surface flow acceleration/ Sphere displacement	Sphere diameter	3 mm	Stokes (1851), Ćurčić-Blake and van Netten (2006);
	Distance from sphere center to surface	4 mm	[Kroese and Schellart (1992)]
	Water density	998 kg m^{-3}	
Canal flow velocity/ Surface flow acceleration	Canal diameter	350 μm	Sexl (1930), Denton and Gray (1983), van Netten (2006) [Kroese and Schellart (1992);
	Canal fluid viscosity	0.51 Pa s	Weber and Schiewe, (1976); van Netten and Kroese (1987)]
Cupular deflection/ Canal flow velocity	Cupula radius	150 μm	van Netten and Kroese (1987), van Netten (1988);
	Cupula sliding stiffness	0.0325 N m^{-1}	[Kroese and Schellart (1992); van Netten and Kroese (1989)]

of the hydrodynamics of the canal and micromechanics of the neuromast create a low-pass filter with cupula deflections that are proportional to flow acceleration at the body's surface over a broad range of low frequencies (van Netten, 2006). Given that the cupula moves as a rigid body, carrying with it the hair bundles projecting from the apical surface of the hair cells (van Netten and Kroese, 1989), these deflections may be interpreted as the input for the neurophysiology of the canal system.

The effect of all levels of biomechanical filtering may be evaluated by comparison with neurophysiological measurements. The levels of biomechanical filtering yield a measure of the sensitivity as the ratio of cupular deflections to the sphere's displacement, calculated as the product of the following transfer functions (each shown in Fig. 4C and Table 1):

$$\frac{\text{Cupular deflection}}{\text{Sphere displacement}} = \left(\frac{\text{Surface acceleration}}{\text{Sphere displacement}}\right) \left(\frac{\text{Canal velocity}}{\text{Surface acceleration}}\right)\left(\frac{\text{Cupular deflection}}{\text{Canal velocity}}\right). \quad (1)$$

The frequency response of this sensitivity estimates the filtering solely by the biomechanics of the canal system [Fig. 4D(ii)]. Comparing this prediction with the measurements of changes in the action potentials in the lateral line nerve of the trunk in trout (Kroese and Schellart, 1992) illustrates a remarkable congruence of neurophysiology and biomechanics (Fig. 4D). The 40 dB dec^{-1} rise in sensitivity at low frequency demonstrates that cupular deflections are proportional to the acceleration of the sphere [Fig. 4C(ii)]. This is encoded by afferent action potentials permitted by the low-pass filtering of the canal and cupula [Fig. 4C(i)]. A discrepancy between

biomechanics and neurobiology occurs at frequencies above maximum sensitivity, where cupular deflections maintain a constant high sensitivity but afferent action potentials attenuate with frequency. This difference may be attributed to the limitations of neurophysiology at these high rates. The time-constant of mechanotransduction across the membrane of the hair cells creates a 300 Hz cut-off frequency (Hudspeth and Corey, 1977; Kroese and van Netten, 1989) and the afferent neurons encounter reduced sensitivity at 250 Hz and an upper limit of 500 Hz due, respectively, to the relative and absolute refractory periods of action potentials. With this exception, it may be concluded that the filtering of the canal neuromasts is dominated by their mechanical properties and that variation in their morphology enables sensitivity to extend over a broad range of frequencies. This dominant role of mechanics suggests that the canal system may be tuned through differences in the morphology of the cupula and the canal.

Sensing sound

The diversity of auditory systems also presents a compelling comparative platform for sensory biomechanical studies. The biomechanics of the hearing apparatus plays a key role as a primary filter of incident sound signals in examples of biological audition from insects to amphibian and mammalian ears. Here, we discuss the biomechanics of three types of auditory systems found in insects. The sensory biomechanical perspective has also been adopted rigorously in studies of amphibian ears and covered by Gridi-Papp and Narins (2009) (also see Purgue and Narins, 2000a, 2000b).

Johnston's organs

Many insects use antennal or cercal structures to detect air particle vibrations from near-field sound sources. Vibrations of the antennal structures are detected by mechanosensory Johnston's organs embedded within the basal segments of the insect's antenna (Göpfert et al., 1999). Across insects, Johnston's organs have been implicated in several important functions that depend on the sensing of vibrations. These include dection of air-flow (Gewecke and Heinzel, 1980; Heinzel and Gewecke, 1987), flight stabilization (Sane et al., 2007), audition (Robert and Göpfert, 2002; Yorozu et al., 2009), and detection of gravity (Kamikouchi et al., 2009). Here we describe the role of Johnston's organs in audition in mosquitoes, in which the biomechanics of the antennal function appears "tuned" to ecologically important stimuli.

In the case of antennal sound reception, the main feature of the sound stimulus is the particle velocity. This problem has been studied in some detail in mosquitoes (Göpfert et al., 1999; Göpfert and Robert, 2000, 2001; Jackson and Robert, 2006) and Drosophila (Göpfert and Robert, 2002; Robert and Göpfert, 2002; Lu, 2009), also see Göpfert, this issue. In mosquitoes, the flagella of males' antennae (Fig. 5A) are naturally tuned to the wing-vibration frequencies of females (Göpfert and Robert, 2000). The vibrations of the antennal flagellum are transduced by the individual units (called scolopidia) of Johnston's organs into action potentials (Fig. 5B). This method of communication poses a steep physical challenge in mosquitoes due to their small size. Because the female's wing length is about one-sixth of the wavelength of the sound that they produce, wing vibrations produce very little acoustic power and therefore have a limited broadcast range (Jackson and Robert, 2006). Perhaps as an adaptation, male mosquitoes have evolved exaggerated Johnston's organs, with numerous (~16,000) sensory neurons that are capable of responding to flagellar-tip displacements of a few nanometers (Göpfert and Robert, 2000). Furthermore, the plumose structure of males' antennae (Fig. 5A) serves to enhance sensitivity by increasing the total surface area and thereby the drag on the antenna. At the low Reynolds numbers in which it operates, the plumose flagellum acts like a paddle rather than a brush due to low leakiness (Cheer and Koehl, 1987). As a result, the entire flagellum moves as if it were a rigid rod moving about within its pedicellar socket thereby allowing the antennal motion to be transmitted to the basal segments with utmost fidelity. This exquisite nanometer-range sensitivity of the sensory neurons underlying the Johnston's organ's ear is coupled with the hair-like projections on the antennal structure, which ensures a forced damped oscillator-like behavior of the antenna in response to sound (Fig. 5B).

Tympanal organs

In addition to antennal or cercal structures, insects from diverse groups have independently evolved auditory tympanal organs that detect pressure waves from distant sources of sound. These ears are typically comprised of a tympanic membrane connected to a scolopidial organ which houses a chordotonal neuron that detects the vibration of the tympanic membrane (Robert et al., 1994). The case of the parasitoid tachinid fly, Ormia ochracea, and its cricket host offer a particularly illustrative insight into the role of sensory biomechanical processes. In this system, both the host and the parasite depend on audition for their survival. The parasitoid fly locates a host cricket by hearing its chirps. Some time after eggs are laid within the cricket, hatched larvae feed on the host cricket's tissues. Because O. ochracea is small, the two tympanal membranes used in hearing are spaced close together (~1.2 mm) on the ventral prosternum under the neck (Robert, 2001). This means that for the parasitoid fly, both the time difference between the incidence of sound on the two ears (called interaural time difference or ITD, ~1.7 µs,) (Robert, 2001) and the interaural intensity difference (IID, <1 dB) (Robert, 2001) are too small for the underlying chordotonal neurons to make a bilateral comparison as a means of localization. Therefore, the small size of this sensory structure challenges the ability to sense the directionality of the sound. Nevertheless, these insects meet the challenge of locating the positions of their cricket host rather well.

The key to how these tiny parasitoid flies detect the direction of sound is within the biomechanics of a flexible, cuticular intertympanic bridge. This structure mechanically couples the two tympanic membranes such that their vibration can now occur in three distinct modes, depending on the frequency of the incident sound wave. At low frequencies (<3 kHz), the tympanic membranes vibrate together in phase and are unable to establish a sufficient difference in the timing of their vibration to enable localization by sound. However, at an intermediate frequency range (between ~5 and 15 kHz), the phase difference between the two tympanic membranes is large enough to inform the fly about the direction of the sound. At frequencies >15 kHz, the binaural
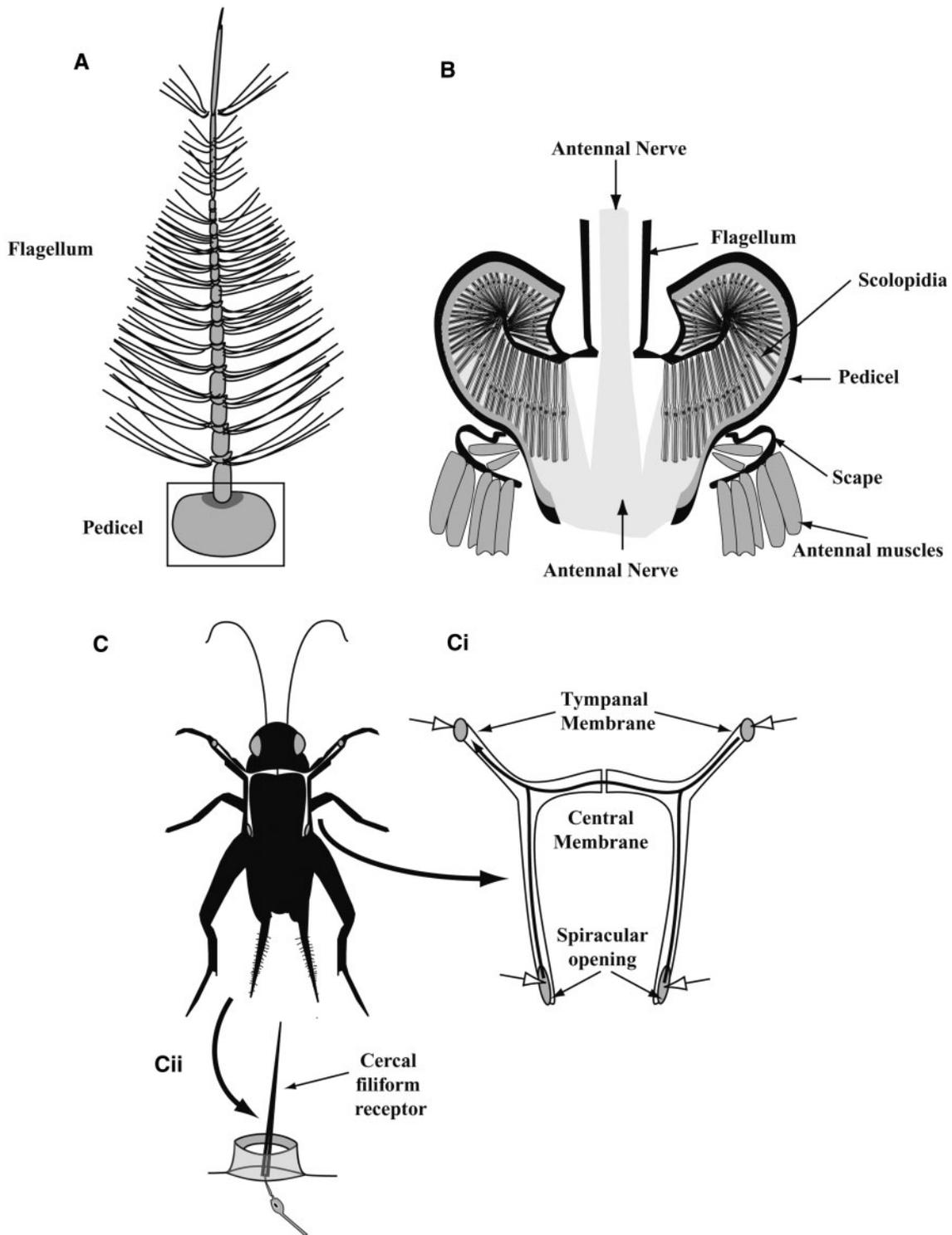
Fig. 5 Antennal and tympanal audition in insects. (**A**) Mosquito antenna. Area marked by the rectangle indicates the location of Johnston's organs. (**B**) Cross-section of the salient feature of Johnston's organs. The scolopidial units, most of which contain two bipolar neurons, connect to the prongs and convey information about the movement of the flagellum relative to the pedicel to the brain through the antennal nerve. (**C**) The cricket auditory and airflow-sensing system. (i) The tympanal ear of the cricket. A pressure wave incident upon the outer face of the tympanal membrane (indicated by white arrows) is compared with the wave incident on the inner face (black arrow) via the tracheal tubes. This enables crickets to determine the location of the source of the sound. (ii) Individual filiform hair sensor present on a cricket's cerci enable crickets to sense ambient air disturbances.

membranes combine the two modes described above such that the contralateral membrane is now effectively silenced and the directionality is determined by the side on which the tympanic membrane is vibrating. Thus, the parasitoid fly is able to biomechanically amplify the binaural ITD and IID and determine from a distance where the singing cricket is located and target it for oviposition (Robert et al., 1992, 1996a, b; 1999; Robert, 2001).

Like her tachinid parasites, the female cricket, *Gryllus bimaculatus*, must also acoustically determine the location of a singing male (Robert et al., 1992; Fig. 5C). Again, this process involves the biomechanics of sound-sensing structures. Unlike the tachinid flies, the tympanic membrane in crickets is located on their pro-thoracic tibiae, rather than in the prosternum [Fig. 5 C(i)]. Sound is conducted to both the outer and inner surfaces of the tympanic membrane from four regions. The outside surface of the membrane receives sound via the external air whereas the inside surface receives it from three other locations via a system of air-filled spiracular tracheal tubes (Fig. 5C). These sound inputs are received at the ipsilateral and contralateral spiracles under the wings on the thorax, and very weakly from the tympanic membrane of the contralateral leg. Thus, the tympanic membranes in crickets act essentially as pressure-difference receivers such that the strains in the tympanic membrane depend on the vector addition of the forces due to sound arriving from these four locations. The ipsilateral and contralateral tracheal tubes are divided by a central membrane, whose mechanics is crucial for enhancing the phase difference between the ipsilateral and contralateral spiracle-conducted sounds (Robert et al., 1994, 1996b; Adamo et al., 1995; Miles et al., 1995; Muller and Robert, 2001).

The study of all the systems described above were primarily enabled by the development of Laser Doppler Vibrometry, which allows researchers to measure fine-scale vibrations as a means of gaining insight into the biomechanical factors involved in hearing by insects.

Biomechanics of non-mechanosensory modalities

Although this review focuses primarily on mechanosensory organs and their interaction with their mechanical environment, sensory biomechanics is by no means restricted to mechanosensors. In the cases of silkworm moths fanning their wings and moths flapping in air, a mechanical modification of the odor is crucial for olfaction. As argued by Loudon and Koehl (2000), the fanning of wings by the silkworm moth, *Bombyx morii* causes an enhanced and periodic influx of the odor pulses akin to sniffing in higher vertebrates. Measurements of this airflow in *Manduca sexta* (Sane, 2006; Sane and Jacobson, 2006) and *Locusta migratoria* (Horsmann et al., 1983) reveal a sharp, near sinusoidal delivery of pulses of air to the mechanosensory cephalic hair, which provides phasic feedback to the motor system for flight. In addition to its function in modulating the sampling frequency and the amplitude of odor delivery, this airflow may be involved in other processes such as convective loss of water and heat (Sane and Jacobson, 2006). In these examples, the study of biomechanics can offer a unique insight into strategies used by animals in enhancing their sensory signals and improving perception.

Technical challenges

As evident from most of the examples above, determining the micro-strains that generate a mechanical signal presents a difficult experimental challenge in the biomechanics of sensory organs. In most cases, the problem involves understanding how the coarsely applied strains or sound stimuli translate into microstrains in the immediate vicinity of a mechanosensory apparatus. Because the deflections of these structures occur at a microscopic or nanometer scale, their direct physical measurements are not always possible. Tools such as single-point or scanning Laser Doppler Vibrometry have proved very powerful in enabling researchers to examine finescale motion with exquisite temporal resolution. In the case of the lateral-line system, interferometry has allowed similar insights into the actual motion of the cupulae in response to external flows (Kroese and Van Netten, 1987). In addition, recent application of Particle Image Velocimetry in the near-field around the bodies of fish (Chagnaud et al., 2006, 2008; Coombs et al., 2007) or insects (Bomphrey et al., 2006) also provides promising insights into sensory function. However, the complicated geometry and anisotropic microstructure of sensory organs makes the experimental determination of the biomechanical filter of the sensory stimulus extremely difficult, making this a very fruitful area of collaboration between engineers and sensory neurobiologists in the near future.

In the absence of a method to directly measure micro-strains, several researchers have used numerical approaches to gain insight into the properties of biomechanical filters. These include, most importantly, the Finite Element Analysis of sensory structures (Hößl et al., 2007) to determine the solid mechanical

contribution to the biomechanical filter, as in the case of spiders' slit sensilla, Computational Fluid dynamics to determine the fluid mechanical contribution as in the case of near-field flow around a fish's body (Barbier and Humphrey, 2009; Rapo et al., 2009), or codes involving a combination of the two to deduce the effects of solid-fluid coupling, as in the case of cupular deflection (McHenry et al., 2008).

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References

Adamo SA, Robert D, Hoy RR. 1995. Effects of a Tachinid Parasitoid, Ormia-Ochracea, on the behavior and reproduction of its male and female field cricket hosts (Gryllus Spp). J Insect Physiol 41:269–77.

Barbier C, Humphrey JAC. 2009. Drag force acting on a neuromast in the fish lateral line trunk canal. I. Numerical modelling of external-internal flow coupling. J Royal Soc Interface 6:627–40.

Barth FG. 2004. Spider mechanoreceptors. Curr Opin Neurobiol 14:415–22.

Barth FG, Ficker E, Federle HU. 1984. Model studies on the mechanical significance of grouping in compound spider slit sensilla (Chelicerata, Araneida). Zoomorphology 104:204–15.

Barth FG, Holler A. 1999. Dynamics of arthropod filiform hairs. V. The response of spider trichobothria to natural stimuli. Philos Trans Royal Soc London Series B-Biological Sci 354:183–92.

Barth FG, Humphrey JAC, Wastl U, Halbritter J, Brittinger W. 1995. Dynamics of Arthropod Filiform Hairs. 3. Flow Patterns Related to Air Movement Detection in a Spider (Cupiennius-Salei Keys). Philos Trans Royal Soc London Series B-Biological Sci 347:397–412.

Barth FG, Wastl U, Humphrey JAC, Devarakonda R. 1993. Dynamics of arthropod filiform hairs. 2. Mechanical-properties of spider trichobothria (Cupiennius-Salei Keys). Philos Trans Royal Soc London Series B-Biological Sci 340:445–61.

Bleckmann H. 2008. Peripheral and central processing of lateral line information. J Comp Phys A 194:145–58.

Bleckmann H, Rathmayer W. 1994. Reception of hydrodynamic stimuli in aquatic and semiaquatic animals. Progress in zoology, Vol. 41. Stuttgart: Gustav Fischer. p. 1–115.

Blickhan R, Barth FG. 1985. Strains in the exoskeleton of spiders. J Comp Physiol a-Sensory Neural Behav Physiol 157:115–47.

Bomphrey RJ, Lawson NJ, Taylor GK, Thomas ALR. 2006. Application of digital particle image velocimetry to insect aerodynamics: measurement of the leading-edge vortex and near wake of a Hawkmoth. Exp Fluids 40:546–54.

Chagnaud BP, Bleckmann H, Engelmann J. 2006. Neural responses of goldfish lateral line afferents to vortex motions. J Exp Biol 209:327–42.

Chagnaud BP, Brucker C, Hofmann MH, Bleckmann H. 2008. Measuring flow velocity and flow direction by spatial and temporal analysis of flow fluctuations. J Neurosci 28:4479–87.

Chapman KM. 1965. Campaniform Sensilla On Tactile Spines of Legs of Cockroach. J Exp Biol 42:191–203.

Cheer AYL, Koehl MAR. 1987. Paddles and rakes – fluid-flow through bristled appendages of small organisms. J Theor Biol 129:17–39.

Cocatre-Zilgien JH, Delcomyn F. 1999. Modeling stress and strain in an insect leg for simulation of campaniform sensilla responses to external forces. Biological Cybernetics 81:149–60.

Coombs S, Anderson E, Braun CB, Grosenbaugh M. 2007. The hydrodynamic footprint of a benthic, sedentary fish in unidirectional flow. J Acoust Soc Am 122:1227–37.

Coombs S, Montgomery JC. 1999. The enigmatic lateral line system. In: Fay RR, Popper AN, editors. Comparative hearing: fish and amphibians, Vol. 11. New York: Springer.

Coombs S, van Netten SM. 2006. The hydrodynamics and structural mechanics of the lateral line system. In: Shadwick R, Lauder G, editors. Fish Biomechanics. New York: Elsevier. p. 103–39.

Ćurčić-Blake B, van Netten SM. 2006. Source location encoding in the fish lateral line canal. J Exp Biol 209:1548–59.

Dehnhardt G, Mauck B, Bleckmann H. 1998. Seal whiskers detect water movements. Nature 394:235–6.

Denton EJ, Gray JAB. 1982. The rigidity of fish and patterns of lateral line stimulation. Nature 297:679–81.

Denton EJ, Gray J. 1983. Mechanical factors in the excitation of clupeid lateral lines. Proc Roy Soc B 218:1–26.

Denton EJ, Gray JAB. 1989. Some observations on the forces acting on neuromasts in fish lateral line canals. In: Coombs S, Görner P, Munz H, editors. The mechanosensory lateral line: neurobiology and evolution. New York: Springer-Verlag. p. 79–97.

Devarakonda R, Barth FG, Humphrey JAC. 1996. Dynamics of arthropod filiform hairs. 4. Hair motion in air and

water. Philos Trans Royal Soc London Series B-Biological Sci 351:933–46.

Dickinson MH. 1990. Comparison of encoding properties of campaniform sensilla on the fly wing. J Exp Biol 151:245–61.

Dickinson MH. 1992. Directional sensitivity and mechanical coupling dynamics of campaniform-sensilla during chordwise deformations of the fly wing. J Exp Biol 169:221–33.

Dijkgraaf S. 1963. Functioning and significance of lateral-line organs. Biol Rev Cambridge Philos Soc 38:51–105.

Dumpert K, Gnatzy W. 1977. Cricket combined mechanoreceptors and kicking response. J Comp Physiol 122:9–25.

Edwards JS, Palka J. 1974. Cerci and abdominal giant fibers of house cricket, acheta-domesticus. 1. Anatomy and physiology of normal adults. Proc R Soc London Series B-Biological Sci 185:83–103.

Field LH, Matheson T. 1998. Chordotonal organs of insects. In: Advances in insect physiology, Vol. 27. p. 1–228.

Flock A. 1965. Transducing mechanisms in lateral line canal organ receptors. Cold Spring Harbor Symp Quant Biol 30:133–45.

French AS, Torkkeli PH, Seyfarth EA. 2002. From stress and strain to spikes: mechanotransduction in spider slit sensilla. J Comp Physiol a-Neuroethol Sensory Neural Behav Physiol 188:739–52.

Gewecke M, Heinzel HG. 1980. Aerodynamic and mechanical-properties of the antennae as air-current sense-organs in locusta-migratoria. 1. Static characteristics. J Comp Physiol 139:357–66.

Gnatzy W, Grunert U, Bender M. 1987. Campaniform sensilla of calliphora-vicina (insecta, diptera). 1. Topography. Zoomorphology 106:312–9.

Göpfert MC, Briegel H, Robert D. 1999. Mosquito hearing: sound-induced antennal vibrations in male and female Aedes aegypti. J Exp Biol 202:2727–38.

Göpfert MC, Robert D. 2000. Nanometre-range acoustic sensitivity in male and female mosquitoes. Proc R Soc London Series B-Biological Sci 267:453–7.

Göpfert MC, Robert D. 2001. Active auditory mechanics in mosquitoes. Proc R Soc London Series B-Biological Sci 268:333–9.

Göpfert MC, Robert D. 2002. The mechanical basis of Drosophila audition. J Exp Biol 205:1199–208.

Görner P. 1965. A proposed transducing mechanism for a multiply-innervated mechanoreceptor (trichobothrium) in spiders. Cold Spring Harbor Symp QuantBiol 30:69–73.

Gridi-Papp M, Narins P. 2009. Environmental influences in the evolution of tetrapod hearing sensitivity and middle ear tuning. Integr Comp Biol 49:702–16.

Grunert U, Gnatzy W. 1987. Campaniform sensilla of calliphora-vicina (insecta, Diptera). 2. Typology. Zoomorphology 106:320–8.

Harris GG, van Bergeijk WA. 1962. Evidence that the lateral-line organ responds to near-field displacements of sound sources in water. J Acoust Soc Am 34:733.

Heinzel HG, Gewecke M. 1987. Aerodynamic and mechanical-properties of the antennae as air-current sense-organs in locusta-migratoria. 2. Dynamic characteristics. J Comp Physiol a-Sensory Neural Behav Physiol 161:671–80.

Heran H. 1957. Die Bienenantenne Als Messorgan Der Flugeigengeschwindigkeit. Naturwissenschaften 44:475.

Horsmann U, Heinzel HG, Wendler G. 1983. The phasic influence of self-generated air current modulations on the locust flight motor. J Comp Physiol 150:427–38.

Hößl B, Bohm HJ, Rammerstorfer FG, Barth FG. 2007. Finite element modeling of arachnid slit sensilla- I. The mechanical significance of different slit arrays. J Comp Physiol a-Neuroethol Sensory Neural Behav Physiol 193:445–59.

Hößl B, Bohm HJ, Rammerstorfer FG, Mullan R, Barth FG. 2006. Studying the deformation of arachnid slit sensilla by a fracture mechanical approach. J Biomech 39:1761–8.

Hudspeth AJ, Corey DP. 1977. Sensitivity, polarity, and conductance change in the response of vertebrate hair cells to controlled mechanical stimuli. Proc Natl Acad Sci 74:2407–11.

Humphrey JAC, Devarakonda R, Iglesias I, Barth FG. 1993. Dynamics of arthropod filiform hairs. 1. Mathematical-modeling of the hair and air motions. Philos Trans R Soc London Series B-Biological Sci 340:423–44.

Jackson JC, Robert D. 2006. Nonlinear auditory mechanism enhances female sounds for male mosquitoes. Proc Natl Acad Sci USA 103:16734–9.

Kalmijn AJ. 1988. Hydrodynamic and acoustic field detection. In: Atema J, Fay RR, Popper AN, Tavolga WN, editors. Sensory biology of aquatic animals. New York: Springer-Verlag. p. 83–130.

Kamikouchi A, Inagaki HK, Effertz T, Hendrich O, Fiala A, Göpfert MC, Ito K. 2009. The neural basis of Drosophila gravity-sensing and hearing. Nature 458:165–71.

Kanou M, Shimozawa T. 1984. A threshold analysis of cricket cercal interneurons by an alternating air-current stimulus. J Comp Physiol 154:357–65.

Kroese ABA, van Netten SM. 1987. The application of incident light polarization microscopy for the visualization of vertebrate sensory hair cells in vivo. J Microscopy 145:309–18.

Kroese ABA, van Netten SM. 1989. Sensory transduction in lateral line hair cells. In: Coombs S, Görner P, Munz H, editors. The mechanosensory lateral line: neurobiology and evolution. New York: Springer-Verlag. p. 265–84.

Kroese ABA, Schellart NAM. 1992. Velocity-sensitive and acceleration-sensitive units in the trunk lateral line of the trout. J Neurophysiol 68:2212–21.

Landolfa MA, Miller JP. 1995. Stimulus-response properties of cricket cercal filiform receptors. J Comp Physiol a-Sensory Neural Behav Physiol 177:749–57.

Leydig F. 1850. Ueber die Schleimkanäle der Knochenfische. Mull Arch Anat Physiol, 170–81.

Loudon C, Koehl MAR. 2000. Sniffing by a silkworm moth: Wing fanning enhances air penetration through

and pheromone interception by antennae. J Exp Biol 203:2977–90.

Lu Q, Rajeswaran PR, Effertz T, Nadrowski B, Göpfert M. 2009. Using *Drosophila* for studying fundamental processes in hearing. Integr Comp Biol 49:674–80.

McHenry MJ, Strother JA, van Netten SM. 2008. The boundary layer and fluid-structure interaction in the superficial neuromast of the fish lateral line system. J Comp Physiol A 194:795–810.

McHenry MJ, van Netten SM. 2007. The flexural stiffness of superficial neuromasts in the zebrafish (Danio rerio) lateral line. J Exp Biol 210:4244–53.

Miller JP, Jacobs GA, Theunissen FE. 1991. Representation of sensory information in the cricket cercal sensory system. 1. response properties of the primary interneurons. J Neurophysiol 66:1680–9.

Miles RN, Robert D, Hoy RR. 1995. Mechanically coupled ears for directional hearing in the parasitoid fly Ormia ochracea. J Acoust Soc Am 98:3059–70.

Mogdans J, Krother S, Engelmann J. 2004. Neurobiology of the fish lateral line: adaptations for the detection of hydrodynamic stimuli in running water. In: Emde GVD, Mogdans J, Kapoor BG, editors. The senses of fish: Adaptations for the reception of natural stimuli. New Delhi: Narosa Publishing House. p. 265–87.

Montgomery J, Coombs S, Halstead M. 1995. Biology of the mechanosensory lateral-line in fishes. Rev Fish Biol Fisheries 5:399–416.

Muller P, Robert D. 2001. A shot in the dark: The silent quest of a free-flying phonotactic fly. J Exp Biol 204:1039–52.

Munz H. 1989. Functional organization of the lateral line periphery. In: Coombs S, Görner P, Munz H, editors. The mechanosensory lateral line. Berlin: Springer-Verlag. p. 285–98.

van Netten SM. 1988. Laser interferometer microscope for the measurement of nanometer vibrational displacements of a light-scattering microscopic object. J Acoust Soc Am 83:1667–74.

van Netten SM. 1991. Hydrodynamics of the excitation of the cupula in the fish canal lateral line. J Acoust Soc Am 89:310–9.

van Netten S. 2006. Hydrodynamic detection by cupulae in a lateral line canal: functional relations between physics and physiology. Biological Cybernetics 94:67–85.

van Netten SM, Khanna SM. 1994. Stiffness changes of the cupula associated with the mechanics of hair-cells in the fish lateral-line. P Natl Acad Sci USA 91:1549–53.

van Netten SM, Kroese ABA. 1987. Laser interferometric measurements on the dynamic behavior of the cupula in the fish lateral line. Hear Res 29:55–62.

van Netten SM, Kroese ABA. 1989. Dynamic behavior and micromechanical properties of the cupula. In: Coombs S, Görner P, Munz H, editors. The mechanosensory lateral line: neurobiology and evolution. New York: Springer-Verlag. p. 247–63.

Palka J, Edwards JS. 1974. Cerci and abdominal giant fibers of house cricket, acheta-domesticus. 2. Regeneration and effects of chronic deprivation. Proc R Soc London Series B-Biological Sci 185:105–21.

Pringle JWS. 1938a. Proprioception in insects I. A new type of mechanical receptor from the palps of the cockroach. J Exp Biol 15:101–13.

Pringle JWS. 1938b. Proprioception in insects II. The action of the campaniform sensilla on the legs. J Exp Biol 15:114–31.

Pringle JWS. 1948. The gyroscopic mechanism of the halteres of diptera. Philos Trans R Soc London Series B-Biological Sci 233:347–84.

Purgue AP, Narins PM. 2000a. Mechanics of the inner ear of the bullfrog (Rana catesbeiana): The contact membranes and the periotic canal. J Comp Physiol A 186:481–8.

Purgue AP, Narins PM. 2000b. A model for energy flow in the inner ear of the bullfrog (Rana catesbeiana). J Comp Physiol A 186:489–95.

Rapo MA., Jiang H, Grosenbaugh MA, Coombs S. 2009. Using computational fluid dynamics to calculate the stimulus to the lateral line of a fish in still water. J Exp Biol 212:1494–1505.

Robert D. 2001. Innovative biomechanics for directional hearing in small flies. Biol Bull 200:190–4.

Robert D, Amoroso J, Hoy RR. 1992. The evolutionary convergence of hearing in a parasitoid fly and its cricket host. Science 258:1135–7.

Robert D, Edgecomb RS, Read MP, Hoy RR. 1996a. Tympanal hearing in tachinid flies (Diptera, Tachinidae, Ormiini): The comparative morphology of an innovation. Cell and Tissue Res 284:435–48.

Robert D, Göpfert MC. 2002. Acoustic sensitivity of fly antennae. J Insect Physiol 48:189–96.

Robert D, Miles RN, Hoy RR. 1996b. Directional hearing by mechanical coupling in the parasitoid fly Ormia ochracea. J Comp Physiol a-Sensory Neural Behav Physiol 179:29–44.

Robert D, Miles RN, Hoy RR. 1999. Tympanal hearing in the sarcophagid parasitoid fly Emblemasoma sp.: The biomechanics of directional hearing. J Exp Biol 202:1865–76.

Robert D, Read MP, Hoy RR. 1994. The tympanal hearing organ of the parasitoid fly ormia-ochracea (Diptera, Tachinidae, Ormiini). Cell Tissue Res 275:63–78.

Sane SP. 2006. Induced airflow in flying insects - I. A theoretical model of the induced flow. J Exp Biol 209:32–42.

Sane SP, Dieudonne A, Willis MA, Daniel TL. 2007. Antennal mechanosensors mediate flight control in moths. Science 315:863–6.

Sane SP, Jacobson NP. 2006. Induced airflow in flying insects - II. Measurement of induced flow. J Exp Biol 209:43–56.

Sexl T. 1930. Über den von E.G. Richardson entdeckten ''Annulareffekt''. Z. Phys. 61:349–62.

Shimozawa T, Kanou M. 1984a. The aerodynamics and sensory physiology of range fractionation in the cercal filiform sensilla of the cricket gryllus-bimaculatus. J Comp Physiol 155:495–505.

Shimozawa T, Kanou M. 1984b. Varieties of filiform hairs - range fractionation by sensory afferents and cercal interneurons of a cricket. J Comp Physiol 155:485–93.

Skordos A, Chan PH, Vincent JFV, Jeronimidis G. 2002. A novel strain sensor based on the campaniform sensillum of insects. Philos Trans R Soc London Series a-Mathematical Physical Engineer Sci 360:239–53.

Stokes GG. 1851. On the effect if the internal friction of fluids on the motion of pendulums. Trans Camb Phil Soc 9:8–106.

Theunissen F, Roddey JC, Stufflebeam S, Clague H, Miller JP. 1996. Information theoretic analysis of dynamical encoding by four identified primary sensory interneurons in the cricket cercal system. J Neurophysiol 75:1345–64.

Theunissen FE, Miller JP. 1991. Representation of sensory information in the cricket cercal sensory system. 2. Information theoretic calculation of system accuracy and optimal tuning-curve widths of 4 primary interneurons. J Neurophysiol 66:1690–703.

Thurm U. 1964. Mechanoreceptors in cuticle of honey bee - fine structure + stimulus mechanism. Science 145:1063.

Van Trump W, McHenry MJ. 2008. The effect of morphological variation on the frequency response of superficial neuromasts in zebrafish (Danio rerio). J Exp Biol 211:2105–15.

Vincent JFV, Clift SE, Menon C. 2007. Biomimetics of campaniform sensilla: Measuring strain from the deformation of holes. J Bionic Engineer 4:63–76.

Weber DD, Schiewe MH. 1976. Morphology and function of lateral line of juvenile steelhead trout in relation to gas-bubble disease. J Fish Biol 9:217–33.

Weis-Fogh T. 1947. An aerodynamic sense organ stimulating and regulating flight in locusts. Nature 164:873–4.

Windsor S, McHenry M. 2009. The influence of viscous hydrodynamics on the fish lateral-line system. Integr Comp Biol 49:691–701.

Yorozu S, Wong A, Fischer BJ, Dankert H, Kernan MJ, Kamikouchi A, Ito K, Anderson DJ. 2009. Distinct sensory representations of wind and near-field sound in the Drosophila brain. Nature 458:201–5.